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Brain Mechanisms Underlying the Subjective Experience of Remembering

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Abstract

The ability to remember events in vivid, multisensory detail is a significant part of human experience, allowing us to relive previous encounters and providing us with the store of memories that shape our identity. Recent research has sought to understand the subjective experience of remembering: what it feels like to have a memory. Such remembering involves reactivating sensory-perceptual features of an event, and the thoughts and feelings we had when the event occurred, integrating them into a conscious first-person experience. It allows us to reflect on the content of our memories, and to understand and make judgments about them, such as distinguishing events that actually occurred from those we might have imagined or been told about. In this review, we consider recent evidence from functional neuroimaging in healthy participants and studies of neurological and psychiatric conditions, which is shedding new light on how we subjectively experience remembering.

Keywords

Recollection, Confidence, Vividness, Hippocampus, Parietal Lobe, Prefrontal Cortex

In search of the subjective experience of remembering

Humans have a remarkable ability to transcend the present moment. With the most minimal of cues, an individual can cast backwards or forwards in time, reliving past events or constructing immersive representations of future ones. These jaunts along a personal timeline can be voluntary or involuntary, intentional or otherwise, and appear to lie within the reach of all human beings, with the possible exception of infants and those who have suffered certain kinds of neurological damage. Projecting itself through time is one of the most remarkable tricks the human mind can pull off.

Scientific accounts of memory often focus on its instrumental value as a storage device. Researchers consider what memory offers the organism functionally, in terms of manipulating cognitive representations over short- and long-term timescales; how it provides a database of experiences from which to plan strategies for the future; and how it might have evolved under various selective pressures. Memory is certainly at its most tractable as a phenomenon when thought of as a mechanism for information storage, whose inputs, outputs and errors can be carefully quantified. Much of what we know about how humans remember has stemmed from this approach, with its concomitant focus on memory's objective, measurable parameters.

But remembering – perhaps foremost among mental processes – also has a phenomenology. In philosophical parlance, there is ‘something that it is like’ to be a remembering being: to be reminded of the past, to be in thrall to it, and to be able to reinhabit it, sometimes in as much vivid detail as the present moment. Memories have qualities that are known to the experiencer. These subjective dimensions also mean that memories are capable of being

represented and shared in a variety of ways: in constructions and artefacts that include the artistic and the literary, but also in the personal narratives that we tell ourselves and communicate to those around us. Memory's precious constructions stay with us as vivid, multidimensional experiences – and sometimes, in the case of intense emotion and trauma, linger for longer than we would like.

Science needs to concern itself with these subjective aspects too. They afford us, as human beings, the selective advantage of being able to reflect on the content of our memories, and to make judgments about them as conscious representations, such as in distinguishing events that actually occurred from those we might have imagined or been told about. This reflective ability enables us to place greater weight on real as opposed to imagined experiences, when adapting our behavior or predicting future outcomes in light of what we have learned. Memory founds an individual's sense of identity, and distortions to its narratives can lead to distress and mental ill-health. Investigating the subjective qualities of autobiographical memories, such as the 'feeling of remembering' (Conway 2009), presents opportunities for understanding how memories differ from other related mental states such as future-oriented cognitions, hallucinations and acts of imagination. There are also likely important individual differences in the extent to which humans can re-experience moments from their pasts, and in the vividness, emotionality, multimodality and temporal sequencing of those representations, including their relationship to the self. The ability to engage in 'mental time-travel' (Tulving 1983) is significant for comparative psychology and neuroscience, with important work ongoing on the extent to which non-

human animals have the ability to relive events from their own pasts – research which in turn provides crucial insights into human brain mechanisms.

Our focus in this review is on the subjective experience of autobiographical memory, defined as that category of episodic memory that relates to the events of our own lives. Previously limited by concerns about self-report and introspection, the cognitive neuroscience of the subjective experience of remembering has made substantial progress in recent years, partly due to the emergence of new methodologies for understanding both subjective experience and brain mechanisms. We have recently argued that such an endeavor will likely benefit from analyses that cut across levels of explanation and incorporate insights from the arts and humanities as well as the neurosciences (Simons et al. 2020). We have described seven levels of analysis at which memory can be understood, and across which it can be useful to draw interdisciplinary connections: the molecular, cellular, neural, cognitive, personal, social and cultural. Although our focus in the present article is on neural mechanisms underlying the subjective (personal) experience of remembering, we would emphasize that any such endeavor will only be as successful as the efforts to describe the experience that the neuroscience is purported to explain. Where such examples illuminate the issues in question, we will adopt them from literature, the arts and other areas of intellectual activity.

Towards a science of the subjective experience of remembering

There is a long history to human beings' fascination with their ability to inhabit their own pasts. In the fourth century BCE, Aristotle analyzed recollection as a

process of re-experiencing an original perception 'conditioned by lapse of time'. Memory was a topic of profound interest to thinkers in the Middle Ages, with the emergence of sophisticated theories that in some ways predate the thought currents of contemporary cognitive neuroscience (Dudai & Carruthers 2005). Central to such thinking was the conception of memory as a faculty whose purpose was to generate alternative representations of reality, a view that is congruent with contemporary theoretical models of the relations between past- and future-related cognitions (Fernyhough, 2012; Addis et al. 2007).

The emergence of scientific psychology in the second half of the nineteenth century gave researchers powerful new methods for investigating the phenomenological features of memories. Scientific efforts were broadly divided between the rigorously quantitative approach of scientists like Ebbinghaus, with their focus on the reproduction of lists of learned syllables, and the more subjective inquiries of Galton and others, who used diaries to record the first-person features of their own memories (Draaisma 2004).

In more recent times, several contemporary scholars have contributed particularly to scientific progress in understanding the subjective experience of remembering. Endel Tulving's (1983) development of the idea of mental time-travel has focused researchers' attention on the cognitive and biological processes that enable an organism to roam across past, present and future. Marcia Johnson's (1993) source monitoring framework understands judgements about what constitutes an act of remembering (as distinct from an imagining or hallucination) as involving the sifting of multiple different sources of information, including the vividness, richness and emotionality of the

representation. Daniel Schacter's work (e.g., Schacter 1996; Schacter et al. 1998) has understood memories as mental constructions that can have vivid subjectivity but that are prone to a variety of reconstructive errors, each of which are telling about the cognitive and neural mechanisms that underpin them (Loftus 2017).

These advances at the cognitive and personal levels of analysis set out some of the *explananda* for understanding the brain mechanisms of the subjective experience of remembering. Before reviewing the relevant neuroscience, we focus on some of the key features of episodic memory that must be brought into any such account.

The reconstructive nature of memory

The narrative form of acts of remembering lends them particularly to literary treatments. In the novels of Toni Morrison (1987) and Kazuo Ishiguro (1995), to take two examples, moments from the past are experienced not as fixed representations but as aggregations of experience that are endlessly recombined and negotiated to meet the exigencies of reality and the needs of the rememberer. Memory in such fictions is an unstable landscape in an unreliably narrated world, in which it can be difficult to be sure of the authenticity of what is being experienced as a representation of the past. This view of memory resonates with the formulation of Lord Byron (1821): 'It is singular how soon we lose the impression of what ceases to be constantly before us... There is little distinct left without an effort of memory, then indeed the lights are rekindled for a moment – but who can be sure that imagination is not the torch-bearer?'

Artistic and literary treatments frequently emphasize this making and remaking of past events in the act of recalling the past. This puts them somewhat at odds with a widespread popular misunderstanding of autobiographical memory as a literal act of *reproduction*, in which a representation of an event can be summoned back into consciousness like the playing of a mental DVD. The insights of writers such as Morrison and Ishiguro are more closely aligned with scientific models of memory as an act of *reconstruction*, in which representations of past events are assembled at the time of recall under the influence of varied biases and pressures, some of which have little to do with the remembered event. Continuing the literary theme, contemporary research into autobiographical memory views it as an act of storytelling by a brain that can integrate multiple sources of relevant information, but which does not store fixed representations or neural ‘files’ corresponding to the event in question.

On the reconstruction view, remembering involves reactivating sensory and perceptual features of an event, and the thoughts and feelings we had when the event occurred, integrating them into a conscious first-person experience. One significant problem for cognitive neuroscience is to explain how these processes occur across the many different neural systems involved in autobiographical memory. A further challenge concerns the ‘cognitive feelings’ (Conway 2009) which distinguish memories from representations of other counterfactual scenarios such as envisaged future events (Schacter et al. 2007) or acts of imagination (Johnson et al. 1993). Why are memory constructions experienced subjectively as memories, rather than as something else? How does our confidence in such judgments dissociate from

their veridicality? How do such attributions break down in neurological or psychiatric states, such as confabulation or delusion? Recent evidence allows such questions to be addressed as part of an account of the subjective experience of remembering.

The multisensory experience of remembering

Another conundrum for a neuroscientific account of remembering is to explain how memories can incorporate multiple streams of sensory information. The novelist Virginia Woolf's description of her earliest memory, for example, from her autobiographical 'A Sketch of the Past' (Woolf 1985), incorporates tactile, auditory and visual impressions in conjunction with feelings and cognitions: 'hearing the waves breaking ... seeing this light, and feeling ... the purest ecstasy I can conceive' (p. 64). This multisensory quality of the psychology of remembering presents a challenge to attempts to understand memory's underlying neural mechanisms, given how sensory processing in the brain is spread among distinct (and in some cases relatively distant) anatomical systems. Somehow the variety of sensory information that has to be incorporated into a memory representation must be brought together and integrated across neural systems in creating the distinctive subjective experience of remembering.

Memory and the self

Autobiographical memories do not only give us a rich multimedia experience; they also come with a distinct sense that they are relevant to our own self, rather than to anyone else. As William James (1890) wrote: 'Memory requires

more than mere dating of a fact in the past. It must be dated in *my* past.' This feature of memory has inspired important theoretical work in psychology on the relation between autobiographical memory and the autobiographical self (Conway & Pleydell-Pearce 2000). The processes by which memories are associated with the self are strongly modulated by social processes, such as in conflicts among adult siblings around memories of a shared childhood, which can lead to one sibling claiming a memory that actually 'belongs' to the other (Sheen et al. 2001). More serious distortions to the associations between memory and the self have been linked to severe mental disorders such as psychosis and schizophrenia (Frith & Done 1989), and with hallucinatory states in which crucial self-related contextual information is sheared off from the memory construction, leaving the 'free-floating' mnemonic representations that are distinctive of trauma (Hardy et al. 2005).

First-person perspective

Memory tells its stories from different points of view. Most commonly we re-experience the past from the perspective we adopted when living through the original events: that is, from our perspectives as first-person observers. In *The Prelude*, for example, William Wordsworth (1850) observed: 'Oh! many a time have I, a five years' Child, / ... / Made one long bathing of a summer's day, / Bask'd in the sun, and plunged, and bask'd again.' Not all memories are experienced from the point of view of the original experiencer, however. Another form of autobiographical memory includes a third-person perspective on the self as a participant in events, a finding that interested Sigmund Freud

in his discussion of the reconstructed nature of what he called 'screen memories' (Freud 1975).

Building on these early insights, a significant contribution to the psychological study of the subjective experience of remembering came with empirical findings of a distinction between *field* (first-person) and *observer* (third-person) memories (Nigro & Neisser 1983). First-person autobiographical memories tend to be rated higher on subjective vividness, sensory detail, and emotional intensity, whereas remembering the objective circumstances of an event leads to relatively more third-person memories. Any account of the brain mechanisms of remembering faces a challenge to explain how memories can be experienced from these two primary perspectives, along with findings that such perspectival features are modulated by emotion (Robinson & Swanson 1993).

Social and cultural influences on memory

One area of burgeoning research interest has concerned how episodic memories are constructed under the influence of various social and cultural forces. In the example already discussed, social processes around sibling memory disputes have been shown to shape individual memory accounts in powerful ways. Other phenomena with implications for the subjective experience of remembering are social contagion (Harris et al. 2017), memory conformity (Maswood et al. 2019) and collaborative remembering (Rajaram 2011). Questions about the phenomenology of remembering are also relevant to the growth of research into collective memories (Hirst et al. 2018). When memories are shared across social and cultural groups, questions arise about

the extent to which they can be described in terms of their subjective, person-centered qualities. If they can, the processes involved in creating such distributed experiences need to be brought into the scientific account. Similarly, autobiographical memory appears highly sensitive to cultural and contextual differences (Wang 2016). If we are to ask the ‘What is it like?’ questions about the first-person experience of memory, it appears that we must strive towards explanations pitched at the social and cultural as well as the personal and cognitive levels of explanation.

Methodologies for studying subjective experience

If the phenomenology of remembering has only relatively recently become tractable to scientific inquiry, one reason for the delay is likely to be well-known difficulties with the empirical study of subjective experience. As noted, qualitative studies of memory have traditionally relied on self-report and diary methods. Such prospective or retrospective reports, of the kind often produced in pre- or post-scan interviews (St. Jacques & De Brigard 2015), are themselves susceptible to reconstructive errors, as well as being subject to biasing expectations about ‘normative’ memory performance, along with self-theoretical assumptions about what kind of memory the respondent has.

Potentially more reliable are methods for sampling experience that try to capture acts of remembering as they unfold. A drawback to such approaches is their potential to disrupt the free flow of unconstrained recall, in addition to the challenge of integrating sampling methods with neuroscientific techniques such as neuroimaging, with the risk of probe stimuli introducing artefacts into hemodynamic or EEG signals. Some of these pitfalls have

begun to be addressed in recent work with Descriptive Experience Sampling (DES), a method in which, through an iterative process involving repeated sampling of moments of experience followed by expositional interviews, participants gain expertise in reporting what was in their experience at the moment just before they heard a beeper sound. Successful integration of this method with fMRI has shown its potential as a method for obtaining more nuanced descriptions of experience than have previously been possible in neuroimaging studies (e.g., Fernyhough et al. 2018). Another promising methodological avenue involves free recall of narrative videos, in which participants watch a movie and then verbally describe the events that took place in the movie while being scanned with fMRI (e.g., Chen et al. 2017; Baldassano et al. 2017). Challenges remain, however, including the caveat that even the most careful experience-sampling or recall method involves a necessary time lag between experience and report, and thus a residual risk of reconstructive errors.

These endeavors have come at a time of renewed interest in the more general problem of integrating subjective and neural data on human experience. To date, there has been little work specifically harnessing these new integrated methods to the study of autobiographical memory, but they offer promise for new multilevel understandings of the processes of remembering (Simons et al. 2020). They may also be particularly relevant for challenging assumptions about the unitary, serial nature of experience. Again, literary and artistic models are helpful here. One of the greatest insights of Marcel Proust's masterpiece, *À la Recherche du Temps Perdu* (*In Search of Lost Time*) is that memory always operates with a dual perspective: the point

of view of the rememberer held in relation to that of the original experiencer (Shattuck 1983). One profound implication for research in this area is that, if the subjective experience of remembering can be described with sufficient detail and precision, it may reveal itself to operate at multiple simultaneous temporal scales. Understanding these complexities of the subjective experience of remembering, and integrating them across levels of analysis, will require continued methodological progress.

Understanding the brain mechanisms of remembering

A common approach in cognitive neuroscience research is to ascribe distinct cognitive processes to individual brain regions. Such a region-focused approach originates from neuropsychological studies of patients with focal brain damage, where specific profiles of cognitive dysfunction have been attributed to damage in a particular brain area. With neuroimaging have come new opportunities to study regional specialization across the entire brain, allowing researchers greater flexibility in comparing and contrasting the cognitive functions of different brain regions. In addition, findings from neuroimaging have cast light on brain regions not previously considered to be important for memory, such as the lateral parietal cortex. In line with a region-focused approach to episodic memory, recent studies have revealed interesting dissociations in how distinct brain regions contribute to the processes of recollection. For instance, in one study, brain activity was recorded while participants reconstructed the visual details of composite scenes linking an object to a particular scene location, color, and orientation. The results revealed a dissociation between hippocampal and lateral parietal

contributions to recollection: whereas hippocampal activity was associated with their general success in retrieving event features, left lateral parietal cortex activity tracked the specificity with which individual features were reconstructed (Richter et al. 2016; see also, Cooper et al. 2017). Other studies have linked hippocampal activity to the overall vividness of episodic simulation and lateral parietal activity to the total number of event details generated (Thakral et al. 2017a, 2020), again suggesting a distinction between the construction of an event and rendering its specific details. We review other such dissociations as we consider below the roles of three brain regions whose contribution to the subjective experience of remembering has only recently become apparent: the hippocampus, lateral parietal cortex, and anterior prefrontal cortex.

In recent years, there has also been growing interest in understanding the roles of brain *networks* in remembering (Ranganath & Ritchey 2012; Simons & Spiers 2003). This is not a new idea: it has been long hypothesized that intact memory function depends on communication among brain systems (Luria 1965; Warrington & Weiskrantz 1982). Neuroimaging has since revealed that episodic memory is associated with activity in a diverse set of brain regions including the hippocampus, parahippocampal cortex, retrosplenial cortex, left lateral parietal cortex, posterior cingulate, precuneus, and medial prefrontal cortex. As part of the default network, this posterior medial system has been described as a core network for episodic construction (Addis et al. 2007), recollection (Rugg & Vilberg 2013), and contextual processing (Ranganath & Ritchey 2012). In the context of memory, the posterior medial system is thought to support key aspects of the

subjective experience of remembering — namely, reconstructing multimodal event features into a vivid, cohesive recollective experience (Addis et al. 2007; Ritchey & Cooper 2020; Rugg & Vilberg 2013). The functions of these regions appear to be interdependent: they are consistently co-activated with one another and functionally connected during episodic tasks (Cooper & Ritchey 2019; Geib et al. 2017; King et al. 2015; Schedlbauer et al. 2014). They also exhibit strong functional connectivity with one another during the resting state (Andrews-Hanna et al. 2010). Moreover, functional connectivity of this network has been shown to correlate with retrieval of contextual source information (King et al. 2015; Schedlbauer et al. 2014), memory vividness (Geib et al. 2017), and memory precision (Cooper & Ritchey 2019), with the hippocampus acting as a hub for memory-dependent interactions (Geib et al. 2017; Schedlbauer et al. 2014).

Recently, there have been calls to integrate region- and network-based approaches to understanding the neural bases of episodic memory (Cabeza et al. 2018; Cowell et al. 2019; Ritchey & Cooper 2020). For instance, although the overarching process of recollection appears to be most strongly associated with an integrated network of regions, the unique contributions of individual regions might be understood by mapping out the component operations and representations of recollection (Cowell et al. 2019). Distinct brain regions affiliate with one another during particular cognitive tasks, forming process-specific alliances (Cabeza et al. 2018), with some alliances appearing to be relatively stable across tasks whereas others may be more task-dependent. Due to the flexibility of network interactions, it may be that searching for one-to-one mappings would be insufficient to explain the

relationships between cognitive functions and brain regions: an individual brain region might make distinct contributions to cognition depending on its neural context (McIntosh 2000), with different connections mediating different functions (Davis et al. 2017), and some cognitive functions may be best understood as emerging from inter-regional and inter-network interactions (Fernyhough 2010; Luria 1965). Here, we take a hybrid approach, considering the unique contributions of individual brain regions to recollection, while also considering their relationships across the dynamic process of remembering. Although the hippocampus, lateral parietal cortex, and anterior prefrontal cortex appear to support partially distinct components of recollection, it is through their flexible interaction that these components give rise to a full-fledged recollective experience.

Hippocampus

The hippocampus has long been understood to be crucial for normal memory functioning. Bilateral damage to the hippocampus and its surrounding medial temporal cortex results in severe memory deficits (Scoville & Milner 1957), marked by impairments in forming new memories and in retrieving the specific details of past events. Since the first discovery of the close connection between the hippocampus and memory processes, we have learned a great deal about its contributions to episodic memory and, specifically, the experience of recollection (Eichenbaum et al. 2007; Montaldi & Mayes 2010). Here, we review evidence indicating that the hippocampus acts to bind together the features of an event, including its spatial and temporal context, and supports the access and reactivation of these features

during retrieval. In doing so, the hippocampus provides the informational foundation for the subjective experience of remembering.

Binding of contextual details

The hippocampus supports the formation of flexible associations between different things that co-occur in space and time (Cohen & Eichenbaum 1993) — for instance, remembering who was at a party, where it was, what kind of music was playing, and so on. Patients with hippocampal damage are impaired at remembering the contextual associations of an event (Spiers et al. 2001; Yonelinas 2002) and other forms of relational processing (Konkel et al. 2008), even when they are able to recognize which individual items they have seen before. Parallel findings from neuroimaging studies have linked the hippocampus specifically to associative memory processes (e.g., Giovanello et al. 2004). Through its associative function, the hippocampus indexes an integrated representation of the relationships among specific event features (Ekstrom & Yonelinas 2020). Central to these representations is the spatial and temporal context in which the event occurred. An event's spatial and temporal contexts often serve as the scaffolding that attaches other event features (Ekstrom & Yonelinas 2020; Robin 2018): we remember not only that two items co-occurred, but how they were positioned in space or time relative to one another. Spatial codes in the hippocampus are allocentric, containing information about features in the environment relative to one another rather than to one's own viewpoint. Through this allocentric coding scheme, the hippocampus has been described

as representing a ‘cognitive map’ of the environment (O’Keefe & Nadel 1978) that can be used to bind and organize the features of experience.

Although the spatial functions of the hippocampus have long been appreciated, more recent work has highlighted the role of time in organizing episodic representations in the hippocampus (Davachi & DuBrow 2015; Eichenbaum 2014). In rodents, hippocampal firing patterns are modulated by time (Eichenbaum 2014), and in humans, patterns of hippocampal activity are sensitive to the temporal structure of events (Davachi & DuBrow 2015; Hsieh et al. 2014). This time sensitivity has functional consequences: changes in hippocampal activity at event transitions predict memory for the preceding events (Baldassano et al. 2017; Ben-Yakov & Dudai 2011) and influence memory for temporal information (Davachi & DuBrow 2015), suggesting a mechanism by which recent experiences are carved into memorable episodes that can be replayed during recollection. Indeed, at the time of retrieval, hippocampal activity patterns recapitulate the spatial and temporal similarities of real-world events (Nielson et al. 2015) (Figure 1A). Together, these lines of evidence suggest that the hippocampus binds the features of experience along dimensions of space and time, providing a basis for the sense of mental time-travel that accompanies recollection.

INSERT FIGURE 1 ABOUT HERE

Accessing and reactivating event features

So far, we have discussed how the hippocampus represents the relationships between event features and the specific episodic context of

memories. But how is this information leveraged to support the subjective experience of remembering? By providing relational structure, the hippocampus supports the access of event representations given a partial cue, followed by reactivation of the other details of the event through pattern completion (Marr 1971; Norman & O'Reilly 2003). Consistent with this idea, activity in the hippocampus has been especially linked to the access of episodic memories — that is, the moment of 'ecphory' in which an existing memory is brought to mind — showing an increase in activity as participants successfully retrieve a memory in response to a cue (Addis et al. 2007; Daselaar et al. 2008; Vilberg & Rugg 2012) (Figure 1B). This initial phase of memory access (or construction, as it is sometimes called) is followed by a period of elaboration as memory details are maintained in memory. The hippocampus tends to be less involved in this latter phase, which instead recruits prefrontal, lateral parietal, and/or medial parietal regions (Addis et al. 2007; Daselaar et al. 2008; Vilberg & Rugg 2012). This dissociation parallels other evidence linking hippocampal activity to the general success of associative retrieval, whereas activity in medial and lateral parietal regions was associated with qualitative aspects of recollection (Richter et al. 2016). Notably, similar temporal dissociations emerge during imagination of future events (Addis et al. 2007), suggesting that the hippocampus may be involved in accessing and integrating details that inform any episodic representation, not only memories (see also Hassabis & Maguire 2007). Access of hippocampal representations may also inform the perception of ongoing events, as memories are called to mind to update understanding of the present based on the past (Chen et al. 2016).

As a memory is retrieved, the hippocampus coordinates the reinstatement of its features represented in cortical areas (Carr et al. 2011; Norman & O'Reilly 2003). Previous experiences are 'replayed' through the sequential firing of hippocampal cells that represent the trajectory of recent experience (Carr et al. 2011). Hippocampal replay is thought to facilitate memory consolidation and retrieval, and replay-like activity has been shown to support the successful retrieval of event sequences (Thavabalasingam et al. 2019; Wimmer et al. 2020). As events are retrieved, their specific features are reinstated in cortical regions involved in their representation. For instance, remembering a scene involves activity in scene-selective regions, remembering a face involves activity in face-selective regions, and so on (e.g., Polyn et al. 2005). In support, neuroimaging studies have shown evidence for the memory-related reactivation of cortical brain patterns associated with specific events (e.g., Staerens et al. 2013, Bonnici et al. 2016, Chen et al. 2017). When recall is extended over time, as in real-world instances of remembering, transient reactivation of content-selective areas follows along with the contents of dynamic recall (Gilmore et al. 2021). Importantly, cortical reactivation has been shown to be mediated by retrieval-related activity in the hippocampus (Horner et al. 2015; Ritchey et al. 2013; Treder et al. 2021), and its relation to the subjective experience of recollection depends on the integrity of the hippocampus (Elward et al. 2021). The features of memory are reactivated in a cohesive manner, with the hippocampus supporting incidental reactivation of non-target associations that have been integrated in memory, consistent with a pattern completion account (Horner et al. 2015) (Figure 1C). In a recent study, Treder and colleagues

investigated the timing of hippocampally-mediated reactivation through intracranial EEG, finding that peak hippocampal firing marked the transition from cue representation to target reactivation (Treder et al. 2021).

Interestingly, target reactivation was followed by an increase in activity in medial parietal, medial prefrontal, and lateral parietal areas, suggesting the engagement of these regions in elaborating on the reactivated contents of episodic memory.

In sum, the hippocampus acts to bind together distinct features of an episodic memory, organizing memories around space and time to produce an allocentric ‘cognitive map’-like representation. These bound representations provide the necessary support structure for accessing individual memories and reconstructing their specific event features — processes that are sufficient for successful performance on many laboratory-based memory tasks, such as source memory or cued recall. However, when it comes time to elaborate on the details of the memory, other cortical areas appear to be recruited, including the lateral parietal cortex, suggesting the need for extra-hippocampal processes to support the sustained subjective experience of episodic memory.

Lateral parietal cortex

With the advent of functional neuroimaging, evidence has rapidly accumulated that cortical brain regions beyond the hippocampus might play an important role in episodic memory, one such region being the left lateral parietal cortex, particularly the area around the left angular gyrus (e.g., Wagner et al. 2005). Although lesions in medial parietal regions have been known for many years

to cause amnesia (Cavanna & Trimble 2006), there are few reports in the neuropsychological literature of memory impairments following lateral parietal lesions. If damage to lateral parietal areas does not result in amnesia, what might explain the frequent observations of angular gyrus activity in healthy volunteers during performance of episodic memory tasks? A number of theoretical accounts have been proposed (Shimamura 2011; Wagner et al. 2005), but recent evidence suggests that left angular gyrus, as part of the posterior medial brain network, might be particularly important for the subjective experience of remembering.

First, it is important to confirm that the absence of reports of amnesia in the parietal lobe neuropsychological case literature is not simply because memory was never properly tested in such patients, and that damage to this region might cause memory impairment that was previously overlooked. A number of studies have found that patients with parietal lobe lesions exhibit intact recognition memory, source memory, and associative memory (Berryhill et al. 2009; Davidson et al. 2008; Simons et al. 2010; Ciaramelli et al. 2017), and can answer questions accurately about autobiographical events they experienced in the past (Berryhill et al. 2007; Davidson et al. 2008). Many of these findings have been replicated in brain stimulation studies involving healthy volunteers that have aimed selectively to disrupt left angular gyrus responses (Bonnici et al. 2018; Thakral et al. 2017b; Yazar et al. 2014). It seems clear that reduced angular gyrus function does not result in amnesia; however, it is not true that memory is completely unaffected in such situations.

Subjective measures, such as confidence and vividness

One way to characterize the memory tasks that appear not to be sensitive to angular gyrus dysfunction is that they typically involve the provision of a specific retrieval cue and can often be accomplished by activating and bringing to awareness a relatively small subset of event features. The retrieval cue might be a target stimulus that was studied previously or a specific question relating to a past episode, and needs only to activate sufficient features to permit a relatively simple response decision to be made, such as that the target stimulus is “old” rather than “new”, or that the actor we saw in a Shakespeare play last summer was named Jill. In such tasks, retrieval success, which depends on a number of factors operating at encoding and retrieval, can be measured objectively by reference to the stimuli that were actually studied or to an independent account of the past experience, and can in many cases be accompanied by little reconstructed conscious awareness of the event as a whole.

Although many laboratory memory experiments involve objective tasks like recognition or source memory that appear not to require intact angular gyrus function, other memory tasks go beyond a simple mapping between cue and stored features to involve the construction of a more detailed, multifaceted representation that brings to conscious awareness a subjective experience of remembering a past event as it unfolded (what Tulving, 1983, called “autonoetic awareness”). Such tasks might require an individual to reflect on the content of a memory to decide whether a stimulus is “remembered” along with associated contextual details, or merely “known” to have been previously encountered. Tasks might require the rememberer to

evaluate the qualitative characteristics of a memory in order to judge its richness, vividness, or one's confidence in its accuracy. Alternatively, they might involve combining distinct forms of information, such as multiple sensory modalities or different spatio-temporal frameworks, into a complex feature network that characterizes an autobiographical experience and enables the individual to "relive" the event as it originally unfolded and to recount it to others.

Whereas medial temporal lobe function underpins both objective and subjective memory, much recent evidence suggests that subjective memory tasks depend additionally on the function of left angular gyrus and surrounding posterior medial brain areas. Neuropsychological and neurostimulation studies focused on dysfunction in this region have observed accurate performance on recognition or source memory tasks but reduced confidence (Ciaramelli et al. 2017; Simons et al. 2010; Yazar et al. 2014) (Figure 2A) and fewer "remember" responses on remember/know tasks (Davidson et al. 2008). Such reductions appear specific to recollection, with confidence in recognition memory and other cognitive abilities unaffected, arguing against a general metacognitive account. Functional imaging experiments involving healthy volunteers have found activity in left angular gyrus, or the more medial precuneus, to be sensitive to qualitative characteristics of retrieved memories, such as their rated vividness or confidence (Kuhl & Chun 2014; Richter et al. 2016; Tibon et al. 2019), and to be greater when recollection is indexed by "remember" rather than source memory responses (Frithsen & Miller 2014; Yu et al. 2012). Patients with parietal damage, whose autobiographical memory is intact when cued by

specific questions about events (Berryhill et al. 2007), exhibit impairment when asked to freely recall the events (Berryhill et al. 2007; Davidson et al. 2008), a result replicated in brain stimulation studies that disrupt angular gyrus function in healthy volunteers (Bonnici et al. 2018; Thakral et al. 2017b).

INSERT FIGURE 2 ABOUT HERE

Multisensory integration of distributed mnemonic features

If angular gyrus contributes to memory by combining distinct forms of retrieved information to construct the kind of complex, multifaceted representation that enables the subjective conscious experience of reliving a past event, the region should be sensitive to tasks that require integrating disparate event features, such as multimodal sensory-perceptual details (Shimamura 2011). Anatomically, angular gyrus is an ideal candidate to integrate mnemonic information relating to multiple sensory modalities, as a connective hub that links distributed sensory association cortices with frontal and medial temporal regions (Seghier 2013). Consistent with this proposal, Bonnici et al. (2016) observed neuroimaging evidence of greater left angular gyrus activity during retrieval of integrated multimodal memories compared with memories that were of only a single modality (Figure 2B). The authors found that a pattern classifier was able to decode individual multimodal but not unimodal memories from activity patterns in angular gyrus and, notably, that classifier accuracy tracked the subjective vividness with which participants rated their memories. In other words, a distinctive multimodal memory representation in left angular gyrus (as measured by the pattern

classifier) was subjectively experienced by participants as a vivid recollection (Bonnici et al. 2016; see also, Kuhl & Chun 2014). Supporting the hypothesis that angular gyrus is necessary for multimodal integration of sensory event features, the ability of participants to retrieve information from multiple modalities, but not from single modalities, was significantly reduced following brain stimulation targeting angular gyrus compared to stimulation of a control region (Yazar et al. 2017).

A sensitivity to multimodal information is also apparent in angular gyrus during performance of semantic memory tasks (Humphreys et al. 2021). In the semantic retrieval literature, angular gyrus has been proposed as a convergence zone between sensory association cortices, based on its activity across a range of modality-specific associations (Binder et al. 2009). During episodic retrieval, angular gyrus exhibits greater activity for multimodal than unimodal memories, whereas during semantic retrieval, statistically equivalent levels of activity are observed for multimodal and unimodal information (Bonnici et al. 2016). This apparent distinction may be attributable to differences in the nature of episodic and semantic memories, with retrieval of unimodal semantic memories likely to involve activation spreading throughout conceptual knowledge networks to associated multimodal details (Patterson et al. 2007), reducing differences between unimodal and multimodal conditions. Further research is necessary to understand the extent to which multimodal angular gyrus activity variations reflect a single underlying function that might be modulated differentially during episodic and semantic processing (Humphreys et al. 2021). In any event, the link between angular gyrus pattern classification accuracy and the vividness of participants'

recollections (Bonnici et al. 2016; Kuhl & Chun 2014) indicates that, in the case of episodic memory at least, angular gyrus plays a key role in the subjective experiencing of our memories as rich, multisensory events (Ciaramelli et al. 2017; Tibon et al. 2019).

Objective measures of memory precision

A challenge with seeking to understand the subjective experience of remembering is that, as with the study of consciousness more generally, much of the evidence comes from self-report measures in which participants are asked to introspect on the nature of their own conscious experience. Individuals might be asked to rate their memories for vividness or confidence. They might be asked to judge whether their memories meet criteria to be classified as “remembered” rather than “known”. They might be asked to freely recall a previous experience, using their own judgment as to which details to include or leave out. As noted in the Methodologies section above, such self-report measures can provide valuable insights into the phenomenology of subjective experience, but they are vulnerable to numerous cognitive biases and demand characteristics. As a result of these issues, it can be difficult to establish the extent to which reported qualities of the subjective experience of remembering map onto objective characteristics of the memory content on which they are based.

To overcome these limitations, recent research has investigated the utility of tasks that go beyond traditional binary measures of objective recollection to involve continuous episodic retrieval measures that can track the precision with which memories are recalled. Such measures can reveal

on a continuous scale the extent to which memories range from high-fidelity, precise reconstructions of previous experiences to less accurate, lower-resolution representations (Brady et al. 2013; Harlow & Yonelinas 2016). Evidence suggests that variation in memory precision may be underpinned by at least partly distinct cognitive and brain mechanisms from those responsible for the binary success vs. failure of memory retrieval (Cooper & Ritchey 2019; Richter et al. 2016). For example, retrieval success and precision can be differentially affected by experimental manipulations (Sutterer & Awh 2016), developmental conditions (Cooper et al. 2017), and age-related cognitive decline (Korkki et al. 2020). Neuroimaging and neurostimulation evidence suggests that different regions of the posterior-medial memory network may contribute to the precision with which memories are retrieved (Cooper & Ritchey 2019; Montchal et al. 2019; Richter et al. 2016). For example, some studies have observed activity in the hippocampus or surrounding medial temporal lobe structures to be sensitive to precision (e.g., Montchal et al. 2019), but Richter et al. (2016) found that the success and precision of episodic retrieval could be dissociated neurally when compared directly in the same statistical model, with retrieval success associated with activity in the hippocampus whereas retrieval precision scaled with activity in left angular gyrus (Figure 2C) (see also, Cooper et al. 2017).

These findings are consistent with the idea that functional interactions between the hippocampus and cortical regions such as the angular gyrus are important for reconstructing precise, detailed memory representations (Ritchey & Cooper 2020). It may be that the hippocampus initiates memory retrieval in response to a retrieval cue, providing a threshold signal denoting

whether the cue succeeds or fails to elicit recollection (Yonelinas 2002). This threshold signal can be sufficient for performing many lab-based memory tasks that are based on binary responses, but for tasks that require more qualitative judgments about the detail of a previous experience, hippocampally-mediated reinstatement of the memory in cortical regions such as angular gyrus may be necessary for generating a precise representation of the integrated episodic content (Richter et al. 2016).

Egocentric spatial frameworks and importance for first-person perspective

As outlined in the Introduction, another element that is so crucial to the subjective experience we have when remembering an event is the first-person perspective from which the reconstructed event typically unfolds in front of us. Evidence suggests that parietal lobe regions may be particularly important for imbuing our memories with this characteristic quality. Studies of spatial navigation have found parietal cortex to support egocentric spatial cognitive functions, in contrast to the allocentric “cognitive map” spatial processes that are associated with the hippocampus (Ciaramelli et al. 2010; Weniger et al. 2009; Zaehle et al. 2007). For example, patients with parietal lobe lesions exhibit deficits on egocentric tests of spatial cognition such as landmark sequencing and route navigation, but are unimpaired on allocentric spatial tasks that involve imagining a map of landmark locations (Ciaramelli et al. 2010; Weniger et al. 2009). In contrast, patients with hippocampal lesions have been found to be impaired on tasks assessing allocentric but not egocentric spatial memory (Holdstock et al. 2000; Rosenbaum et al. 2000). Consistent with the idea that parietal lobe dysfunction may lead to impairment

in egocentric aspects of memory, Berryhill et al. (2010) observed that when patients with parietal lesions recalled past autobiographical events, they were less likely to represent themselves in the scenes that they created, and reported fewer details about their thinking, their emotional states and their own actions during their narratives. Similar findings have been reported in healthy volunteers following inhibitory brain stimulation targeting left angular gyrus, which led to a reduced tendency for participants to report subjectively experiencing autobiographical episodes from an egocentric, first-person perspective (Bonnici et al. 2018).

Neuroimaging evidence links egocentric spatial processing with medial parietal regions such as the precuneus (Hebscher et al. 2018; St. Jacques et al. 2017). For example, when healthy volunteers undertook the landmark sequencing and route navigation spatial cognition tasks mentioned above, significant activity was observed in left medial parietal regions around the precuneus (Rosenbaum et al. 2004). Wolbers et al. (2008) observed activation in the precuneus when participants performed a task in a virtual environment that involved keeping track of the positions of surrounding objects relative to their own bodies. Similarly, when participants were asked to make spatial judgments with respect to themselves or without any self-referential framing, egocentric spatial coding engaged the precuneus whereas allocentric coding was associated with hippocampal activity (Zaehle et al. 2007) (Figure 2D). The precuneus may thus be important for episodic memory by providing an egocentric spatial framework that can be utilized by angular gyrus in constructing its integrated episodic representation. Anatomical connectivity between the precuneus and angular gyrus, via the

occipito-frontal fascicle, has been identified by diffusion-tensor based segmentation and tractography studies (Seghier 2013). In this way, angular gyrus interactions with surrounding structures might support the integration of multimodal memory features within an egocentric framework into the kind of first-person perspective representation that enables the subjective re-experiencing of past events.

Anterior prefrontal cortex

If many of the everyday demands we make of our memory system can be accomplished without requiring the embellished level of awareness that accompanies the subjective experience of remembering, an important question is what adaptive value is gained by constructing the kind of integrated egocentric representation that angular gyrus appears to provide. One possibility proposed by Tulving (1983) is that subjective experience (what he called “autonoetic awareness”) affords the adaptive benefit of being able to reflect on the content of our memories, and to make judgments about the things we remember, such as distinguishing events that actually occurred from those we might have imagined. This ability enables us to weigh more highly real versus imagined events when changing our behavior on the basis of our previous experiences.

Subjective experience as a basis for reality monitoring

Such mnemonic evaluation and judgment abilities are considered to require the recruitment of cognitive control processes that are supported by regions of prefrontal cortex. Several memory-related functional distinctions have been

identified within prefrontal cortex, including between ventrolateral, dorsolateral, and anterior prefrontal cortex. Roles have been ascribed for the ventrolateral region in the specification of retrieval cues and the maintenance of recovered information. For example, Dobbins et al. (2002) identified a region of ventrolateral prefrontal cortex that was active during both semantic processing and source recollection tasks, but not during item recognition, interpreting its likely function in recollection as reflecting the controlled semantic analysis necessary for the specification of effective retrieval cues. This region was differentiated from a more posterior region of ventrolateral prefrontal cortex, which showed significant activity across semantic processing, source recollection, and item recognition tasks, consistent with previous suggestions of a role in lexical/phonological maintenance in working memory (Poldrack et al. 1999). The post-retrieval stage of monitoring and evaluating recovered information has been linked with dorsolateral prefrontal cortex. For example, Henson et al. (2000) operationalized monitoring by contrasting situations in which participants expressed low confidence in their memory with situations in which they were highly confident, observing activation in right dorsolateral prefrontal cortex. Similar results implicating dorsolateral prefrontal cortex were also found when the higher monitoring demands of a source recollection task were contrasted with item recognition, considered to rely more on judgments of familiarity (Rugg et al. 1999). The role played by anterior prefrontal cortex has been more difficult to characterize but, consistent with the involvement of nearby regions in self-referential processing (e.g., D'Argembeau et al. 2007), considerable evidence now points to a key contribution to 'reality monitoring', the particular kind of post-

retrieval evaluation that provides the ability to distinguish self-generated from externally-derived information, which helps us make judgments about whether our memories are real (Johnson et al. 1993; Simons et al. 2017).

According to the Source Monitoring Framework, such judgments about the reality of retrieved experiences are typically based on consideration of their features in the light of characteristics that tend to be associated with different kinds of events (Johnson et al. 1993). A memory that is full of vivid visual details is likely to be real, one that is primarily auditory in nature might reflect an event we were told about by someone else, whereas one mainly comprising traces of self-generated thoughts may well have been imagined. Numerous experiments have explored the brain regions that are sensitive to manipulations of internally- and externally-generated memory features (Simons et al. 2017). For example, participants might be asked to remember whether familiar word pairs were previously presented in full (e.g., 'Romeo and Juliet') or whether the second word had to be imagined (e.g., 'Romeo and ?'). Such judgments between real and imagined information are consistently associated with activity in medial aspects of anterior prefrontal cortex (Kensinger & Schacter 2006; Simons et al. 2006). Similarly, medial anterior prefrontal activity is observed when memory judgments require distinguishing the self-generated thoughts elicited by tasks previously undertaken compared with perceptual features such as the location, size, or time in which stimuli were presented (Dobbins & Wagner 2005; Gilbert et al. 2010; Simons et al. 2005). Furthermore, medial anterior responses are sensitive to judgments of whether tasks were previously undertaken by oneself or another agent (Brandt et al. 2014; Simons et al. 2008) (Figure 3A).

INSERT FIGURE 3 ABOUT HERE

Reality monitoring variability in the general population

Examining the behavioral data from studies of reality monitoring in healthy volunteers, it is clear that there is a great deal of variability in performance, with some people able to distinguish self-generated and externally-derived information relatively successfully and others performing much more poorly (Buda et al. 2011). Evidence indicates that these individual differences in the general population may have a specific brain structural basis in the medial anterior prefrontal cortex, the region identified as functionally involved in the neuroimaging data considered above. There are a number of structural landmarks in the brain that emerge relatively late in development and, due to a combination of genetic and environmental influences, exhibit considerable individual variability in the general population (Van Essen 1997). One such structural variation in the medial prefrontal cortex is the paracingulate sulcus which, as a tertiary sulcus, is one of the last sulci to develop *in utero*, varying considerably in size between individuals (Paus et al. 1996) (Figure 3B).

Healthy adults whose structural brain scans indicate absence of the paracingulate sulcus in both hemispheres exhibit significantly reduced reality monitoring performance compared with people who have a prominent paracingulate sulcus on at least one side of the brain (Buda et al. 2011) (Figure 3C). Reduced sulcal folding may reflect weakened intra- and inter-regional connectivity (Van Essen 1997). This suggests that individual differences in reality monitoring ability may be attributable to variations in

functional brain network connectivity between the medial prefrontal cortex and posterior cortical regions (such as angular gyrus) which are involved in processing the multisensory feature representations that enable the subjective experience of remembering (Fornito et al. 2012).

Hallucinations and schizophrenia

Disturbed awareness of what is real may also underlie some of the symptoms of psychiatric conditions such as schizophrenia, in which a person's relation to reality can be altered in ways that disrupt their everyday functioning. Between 60% and 80% of patients with schizophrenia experience frequent hallucinations (Slade & Bentall 1988), for example hearing a person speaking when there is nobody there. Activity associated with hallucinations is often observed in auditory and visual sensory processing areas (Zmigrod et al. 2016), suggesting that part of the explanation for hallucinations may be self-generated sensory experiences that are unusually vivid, such that they resemble the features typical of real events. However, differences are also found in medial anterior prefrontal areas around the paracingulate sulcus in schizophrenia, consistent with an additional difficulty with discriminating self-generated and externally derived information (Frith & Done 1989). People with schizophrenia are often impaired on reality monitoring tasks (Bentall et al. 1991; Brébion et al. 2000), tending to misattribute imagined stimuli as real (Stephane et al. 2010; Vinogradov et al. 1997), an effect that is associated with reduced activity in anterior prefrontal cortex (Garrison et al. 2017; Vinogradov et al. 2008). Moreover, the occurrence of hallucinations in people with schizophrenia can be predicted on the basis of paracingulate sulcus

length, with sulcal reductions in individuals with a history of hallucinations compared with those who received their diagnosis based on other symptoms (Garrison et al. 2015; Rollins et al. 2020) (Figure 3D).

Conclusions and future directions

We began by itemizing five aspects of the subjective experience of remembering that a scientific account must endeavor to explain: its reconstructive nature, its multisensory qualities, its relation to the self, its capacity to adopt both first-person and third-person perspectives, and its sensitivity to social and cultural influences. We conclude by considering how well current cognitive neuroscientific models can account for these features, and how existing gaps in scientific understanding might direct future research.

First, with regard to the reconstructive nature of memory, we have reviewed findings implicating a posterior medial subsystem of the default network in processes generating vivid, cohesive memory reconstructions. The research reviewed supports the idea of the hippocampus as providing the informational foundation for the subjective experience of remembering, with particular roles in binding of contextual details and accessing and reactivating event features in a cohesive way. These functions may be contrasted with the role of the left lateral parietal cortex in guiding the specificity of feature reconstruction. These processes are further supported by distinct prefrontal cortical areas, such as areas of ventrolateral prefrontal cortex (with roles in the specification of retrieval cues and the maintenance of recovered information), and dorsolateral prefrontal cortex (implicated in the post-retrieval stage of monitoring and evaluating recovered information).

Secondly, the multisensory qualities of a subjectively experienced episodic memory appear to result from the integration of information from sensory representational areas with other event features. A specific region of left lateral parietal cortex, the area around the angular gyrus, is anatomically well placed to receive information from sensory areas, and has been strongly implicated in the integration, in functional interaction with the hippocampus, of disparate forms of mnemonic information in creating the complex, multifaceted representations that enable the subjective experience of reliving a past event.

With regard to the self-related quality of episodic memories, a key process is the distinction between internally- and externally-generated sources of information, in which medial areas of anterior prefrontal cortex have been strongly implicated. These neural substrates appear significant for recognizing that a memory representation happened to one's own self, as opposed to being an imagined event or an experience that happened to another person.

Our fourth aspect of subjective experience, the perspectival feature of an autobiographical memory, likely depends on egocentric spatial frameworks associated with medial parietal regions such as the precuneus, contrasting against the allocentric cognitive map-like representations afforded by the hippocampus. These frameworks underlie the first- or third-person perspectives adopted in an episode of remembering, and likely constitute one of the sources of information utilized by the angular gyrus in constructing integrated, multimodal representations of past events.

Evidence relating to the fifth aspect, sensitivity to social and cultural influences, is currently in shorter supply. We have proposed that further advances in understanding the subjective experience of remembering will benefit from an interdisciplinary approach capable of incorporating findings from seven distinct levels of analysis: the molecular, cellular, neural, cognitive, personal, social and cultural (Simons et al. 2020). Although progress has been made in understanding cognitive mechanisms in social memory processes such as collaborative remembering (Rajaram 2011), social contagion (Harris et al. 2017) and memory conformity (Maswood et al. 2019), there is currently only limited evidence on neural mechanisms specific to social processes in memory. Edelson et al. (2011) reported a distinct brain signature of enhanced amygdala activity and enhanced amygdala-hippocampus connectivity predicting long-lasting but not temporary memory alterations following exposure to the erroneous recollections of a social group. Even in the absence of overt social influences, individuals tend to exhibit largely similar patterns of brain activity during recall of a narrative event (Chen et al. 2017), leaving open the question of what neural processes support the idiosyncratic (versus shared) experience of memory. One's cultural background may additionally influence the way that memories are reconstructed: for instance, individuals from East Asian and Western cultures differ in the way that they incorporate contextual and self-relevant details in memory (reviewed by Gutchess & Huff 2016), suggesting a basis for cultural differences in the subjective experience of memory. Conversely, the link discussed above between paracingulate sulcus reductions and hallucinations in schizophrenia has been found to generalize across patients from Australia,

the United Kingdom, and China (Garrison et al. 2015; Rollins et al. 2020).

With a view to future research in this area, issues such as the phenomenology of collective remembering and cultural influences on remembering will likely require further integration with findings and theoretical concepts at the social and cultural levels of explanation.

Such investigations are likely to require further interdisciplinary methodological advances which may in turn have implications for general endeavors to advance the study of subjective experience. Perspectives from the arts and humanities will likely highlight aspects of the subjective experience of remembering that have so far been invisible to scientific inquiry, such as nuances in the vividness of remembered experience, the framing and reframing of memories in narratives as they unfold over time, and the phenomenology of collective remembering. Sources of evidence such as social history, oral testimony and literary texts can, when incorporated into scientific study design, expand the range of questions that scientists can ask about memory (Simons et al. 2020), while further advances in techniques such as experience sampling promise to enrich the qualitative and quantitative data with which scientists can work, such as describing multiple, parallel streams of experience containing both internal and external foci of attention (Ferryhough et al. 2018).

While beyond the scope of this article, it is also important to consider the developmental implications of what has been learned and what remains to be discovered about the neural underpinnings of the subjective experience of remembering. Assessing the subjective experience of remembering in childhood is fraught with difficulties, including infantile amnesia and

methodological issues such as language and task demands. Research has shown that young children can report vivid autobiographical memories with all of the subjective aspects considered here (Bauer 2006), although the integration of processes necessary for vivid, multisensory remembering is rate-limited by a variety of developmental factors. Childhood memory narratives are also powerfully shaped by sociocultural influences including parental conversational style (Reese et al. 1993) and cultural differences (Wang 2006). Developing source-monitoring capacities (Lindsay et al. 1991) and cortical maturation (Bauer 2006) are likely to shape children's subjective experience of remembering in a dynamic, developmental way, appropriate for a functional systems approach (see below) in which different neural systems interact with each other in flexible ways across development.

Our discussion has emphasized how brain mechanisms of remembering can be understood at the network in addition to the region level of analysis. At the network level, the hippocampus, left lateral parietal cortex, and medial portions of the anterior prefrontal cortex interact strongly as part of the posterior medial subsystem of the default network that is especially involved in tasks involving episodic construction (Ritchey & Cooper 2020; Rugg & Vilberg 2013; Schacter & Addis 2007). Yet compelling evidence for region-specific dissociations (such as between hippocampus and posterior medial cortical regions in recollection), as well as interactions with areas outside of this system (such as the lateral prefrontal cortex), point to the need for a framework for understanding region and network contributions that is sufficiently dynamic and flexible to allow for process-specific alliances (Cabeza et al. 2018) that explain variability in the subjective experience of

remembering. One such framework is provided by A. R. Luria's (1965) conception of *functional systems*, defined as systems of hierarchically organized processes which interact in dynamically changing constellations of elements, such that a specific task can be achieved from moment to moment by differing profiles of interacting subsystems (Fernyhough 2010). This approach stemmed from Luria's dissatisfaction with the 'narrow localizationism' that distinguished early work in neurology, along with the need to integrate neural and cognitive levels of explanation (Fernyhough 2010; Luria 1980).

Functional systems have been proposed as a way of characterizing the 'networks of networks' that underpin functionally complex experiences such as verbally mediated mind-wandering and inner speech (Alderson-Day & Fernyhough 2015). They are distinct from other approaches to understanding brain-wide collaborations among neural systems, such as large-scale brain networks (Bressler & Menon 2010), which are conceptualized in a bottom-up way through data-driven network analysis of activity in brain nodes and hubs. In contrast, the functional systems framework proposes a more top-down approach to postulating interactions among cognitive and neural systems based on theoretical insights as well as cognitive and neural data. Crucially, it also emphasizes how these dynamic interactions among brain systems are shaped by developmental, social and cultural factors (Luria 1965). In understanding how memory operates at the levels of brain regions, networks, and networks of networks, a functional systems approach may prove particularly valuable in understanding developmental change in the subjective

experience of remembering, as well as the reorganization of the memory system that can follow brain damage.

In taking such an approach, we can begin to explain the subjective experience of remembering as arising from dynamic interactions between the functional brain networks that are responsible for different components of episodic cognition, which can be recruited when required to meet the demands of the retrieval situation faced (Figure 4). According to this view, the hippocampus and surrounding medial temporal lobe system reactivate and bind elements of an episodic memory, including its sensory-perceptual features, within an allocentric spatiotemporal context to produce a rapid and relatively sparse representation that is sufficient for many of the everyday demands we make of our memory and, indeed, many lab-based memory tasks. When task instructions or internal goals require us to go further, and to reflect consciously on the content of our memory in order to make judgments about it or to construct a narrative reminiscence about the original event, lateral parietal (especially left angular gyrus) and medial parietal brain areas are recruited to produce a more detailed, multifaceted representation that brings to conscious awareness an egocentric, multimodal subjective experience of remembering the event as it unfolded. Interactions with frontal networks including anterior prefrontal cortex enable the cognitive control processes necessary to evaluate and make decisions about our memory, helping us to keep track of our thoughts, feelings and reflections, and distinguish them from events we may have experienced or been told about by someone else. This valuable ability allows us to understand and learn from

our experiences, and to use them to make sense of the world and guide subsequent behavior.

INSERT FIGURE 4 ABOUT HERE

Remembering has a subjective quality that must figure in scientific accounts of its functioning. This challenge has begun to be met by new methodologies for gathering data on these phenomenological properties, more nuanced design of experimental paradigms allowing separate aspects of the subjective experience of remembering to be teased apart in the laboratory, and a growing understanding of the neural regions, networks, and functional systems that underpin these psychological processes. By considering memory in its deep experiential richness, scientists can hope to make further progress in future years towards an explanation of human beings' capacity to relive, in varying shades of phenomenological color, the most trivial and the most profound moments from their pasts.

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Figure Legends

Figure 1. Hippocampus

- A. At the time of retrieval, hippocampal representations are organized according to the spatial similarity (top) and temporal similarity (bottom) of real-world events. From Nielson et al. 2015.
- B. Hippocampal activity peaks during early phases of autobiographical memory retrieval (top), in contrast to activity in visual cortex, which peaks later as memories are elaborated (bottom). Adapted from Daselaar et al. 2008.
- C. Hippocampal activity is correlated with reactivation of non-target associations during retrieval of an integrated (“closed-loop”) episodic memory. From Horner et al. 2015.

Figure 2. Left Lateral Parietal Cortex

- A. The objectively accurate recollections of patients with lateral parietal lesions are associated with reduced subjective confidence compared with matched control participants. Adapted from Simons et al. (2010).
- B. In left angular gyrus (shown in yellow), greater activity is observed during retrieval of integrated audio-visual memories compared with memories of only a single modality. From Bonnici et al. (2016).
- C. Retrieval success is associated with activity in the hippocampus whereas retrieval precision scales with activity in left angular gyrus. Adapted from Richter et al. (2016).

- D. Allocentric spatial coding activates the hippocampus (shown in red) whereas egocentric spatial coding activates precuneus (shown in blue).
From Zaehle et al. (2007).

Figure 3. Anterior Prefrontal Cortex

- A. Locations of medial anterior prefrontal cortex activity reported by 12 fMRI studies of reality monitoring in healthy volunteers.
- B. Examples of long (left panel) and short (right panel) paracingulate sulci (marked in red). Adapted from Garrison et al. (2015).
- C. Healthy volunteers in whom the paracingulate sulcus is absent in both hemispheres exhibit reduced reality monitoring performance. Adapted from Buda et al. (2011).
- D. Paracingulate sulcus length predicts occurrence of hallucinations in schizophrenia, being reduced in patients who hallucinate whereas there is no difference between those who do not hallucinate and control participants. From Garrison et al. (2015).

Figure 4. Brain Mechanisms of Subjective Remembering

Key regions of interest are shown in bolded font, with important auxiliary regions (medial parietal cortex, which includes precuneus, and sensory regions, processing different modalities of information) also shown. Arrows reflect network interactions supporting communication among these regions.

Figure 1

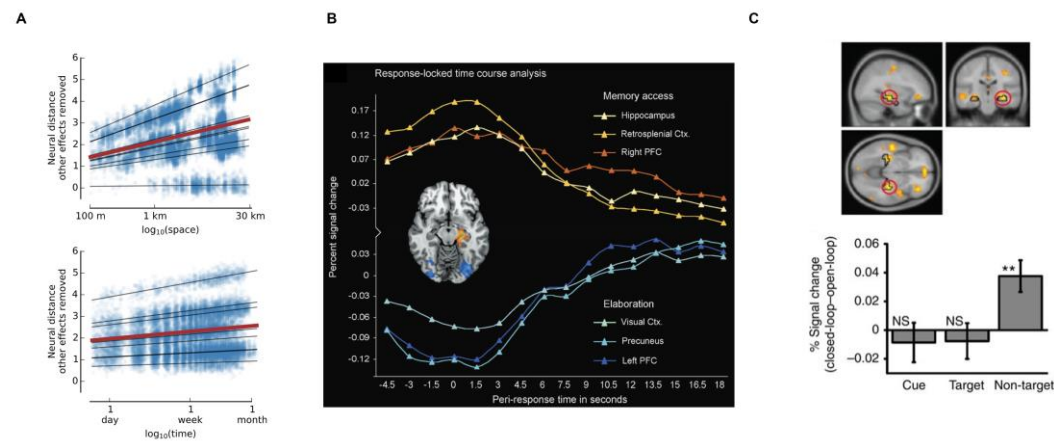


Figure 2

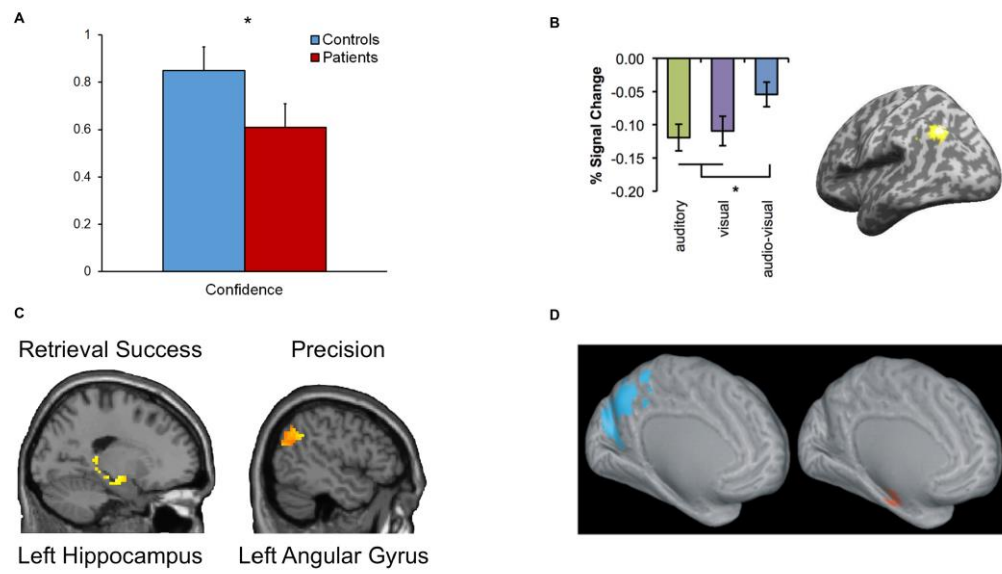


Figure 3

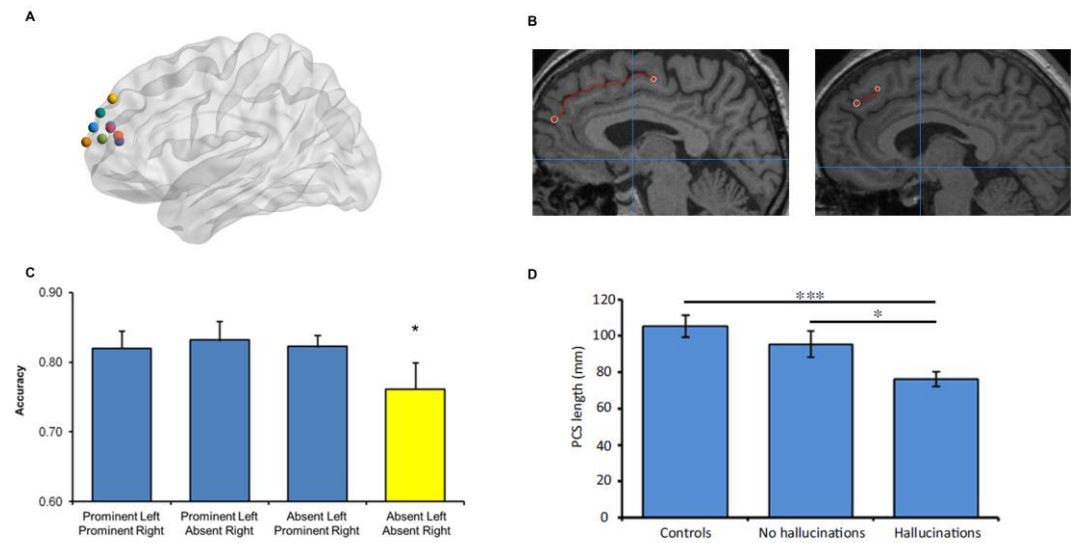


Figure 4

